

**Bulletin of the Museum of Comparative Zoology**

AT HARVARD COLLEGE

VOL. 107, No. 8

---

AIRPLANE OBSERVATIONS OF HOMING PIGEONS

By DONALD R. GRIFFIN

Department of Zoology, Cornell University  
Ithaca, New York

CAMBRIDGE, MASS., U. S. A.

PRINTED FOR THE MUSEUM

December, 1952

MUS. COMP. ZOOLOG.  
LIBRARY

DEC 18 1952

HARVARD  
UNIVERSITY

No. 8.—*Airplane Observations of Homing Pigeons*

BY DONALD R. GRIFFIN

Department of Zoology, Cornell University  
Ithaca, New York

INTRODUCTION

The homing of domestic pigeons and the migrations of wild birds are often considered as comparable cases of natural navigation. In both types of long distance flight it is difficult to discover adequate guiding cues that lie within the sensitivity range of the birds' sense organs. Hence in both cases the theories advanced to explain the birds' orientation have been diverse, speculative, and sometimes fantastic. In other respects the two types of natural navigation are different. Pigeons must be trained; but wild birds train themselves or perhaps learn from their fellows. At least on its first migration a wild bird seeks a goal it has never visited; whereas the pigeon is always returning to a familiar home. Long annual migrations of wild species are linked to seasonal patterns of climate, activity, and reproduction, while pigeons may home at any season and without any immediate incentive other than the attraction of the home loft itself.

The accumulated evidence concerning the sensory basis of navigation in homing pigeons has been reviewed by Claparède (1903), Watson and Lashley (1915), Heinroth and Heinroth (1941) and Griffin (1944). This evidence stems from the most diverse sources, ranging from the anecdotes of pigeon racing enthusiasts to the most painstaking type of scientific experiments, such as those of Sigmund Exner (1905). Fruitful interpretation of even the more carefully controlled experiments is hindered, however, by the rarity of incontestable records of straight flight towards the home loft over territory completely unfamiliar to the pigeons. In most cases the time required for return from distant release points in unfamiliar territory was great enough to leave considerable room for doubt whether, on the one hand, the homing flight had been essentially direct but included stops for rest or other purposes, or on the other hand, might have involved extensive wandering or exploration in search of familiar territory.

Direct observation from airplanes has recently thrown some light on the actual routes which wild birds fly in finding their way home to their nests after being artificially transported to a distance. Herring

gulls and gannets were observed to make exploratory flights in many directions, flights which covered a wide area surrounding the release point and which probably brought the birds, in time, within sight of familiar landmarks (Griffin, 1943; and Griffin and Hock, 1949). Homing by exploration was suggested for pigeons many years ago (Hodge, 1894; Claparède, 1903; Rabaud, 1928; Rivière, 1929; and Gundlach, 1932). It therefore seemed desirable to apply to pigeons the same technique of airplane observation which had been developed for use with wild birds.

Fifteen observation flights over distances up to 100 miles disclosed several cases in which the birds appeared to be relying upon exploration or topographic landmarks. But in other instances there was a definite tendency for the pigeons to head in the approximate direction of home, even when flying over what was almost certainly unfamiliar territory. Despite the fact that no final conclusions can be drawn from the results of these observations, the homing behavior of these pigeons is of interest in view of the scarcity of precise, adequately controlled descriptions of the actual routes between release point and home loft.

Grateful acknowledgement is made to the Office of Naval Research for financial support which permitted the completion of this series of airplane observations in 1947, through a research contract with Cornell University.

## METHODS

The pigeons used in these investigations were the progeny of birds whose previous owners reported rapid homing flights of 100 to 500 miles. The majority were of dark colors, but a number of pure white pigeons were included in the flock since they are much more easily visible from the air. In all of the airplane observations reported below one or more white birds were in the group that was followed. White pigeons are seldom used by pigeon racers, chiefly because they seem to be more susceptible to attacks by hawks. Hence there has not been any intensive selection to develop racing strains of white pigeons, and certainly my white birds showed heavier losses than those of the darker colors.

Of the pigeons mentioned below, Nos. 4-17 were hatched and raised in a loft five miles S.W. of Ithaca, N. Y., while Nos. 34-49 (all white birds) were purchased at an early age and trained with other young pigeons. In all cases the birds were carried to distances which are

customary in races involving pigeons of their age; thus Experiment I employed birds of four and five months in flights of 25 miles or less, while for Experiment II, which included flights from as far as 100 miles, the birds were at least one year old.

The loft was of conventional construction with a one-way entrance or "trap" that allowed the pigeons to enter a small cage where they remained until inspected and allowed into the loft proper. After each release, including all training flights, the loft was visited often enough to ascertain which birds had flown a reasonably straight course home, and which might have remained out long enough for extensive wandering. The daily exercise and training flights at short distances were restricted to the late afternoon, usually to the last two hours of daylight. This set limits to the amount of territory with which the birds could become familiar; and throughout the experiments an attempt was made to minimize the time available for uncontrolled wandering. This effort was not entirely successful, for several birds remained away overnight on one or more occasions during their training; and the maximum time away from the loft is given below for each bird observed from the air.

In airplane observations the same general methods were used as with wild birds (see Griffin, 1943; and Griffin and Hock, 1949); an altitude of 800 to 1000 feet above the ground was maintained and the pigeons scarcely ever flew at altitudes greater than 100 feet. The presence of the airplane at this altitude did not appear to affect the birds' behavior in any way. A single white pigeon, or a group containing a white bird, could be followed without undue difficulty, but the dark colored birds could not be traced successfully except in larger flocks than were available for these experiments. During the preliminary training flights from distances of one to ten miles the birds were accustomed to the presence of aircraft by several releases near airports and by two short flights in which they were observed from the air. Two- or three-place high-wing monoplanes of 65 to 100 horsepower were used for all observations.

The summer and autumn of 1946 were devoted largely to the preliminary training of pigeons for the observations made with yearling birds in 1947. The increase in distance was very gradual so that up to 20 miles the birds were never released more than two or three miles beyond familiar landmarks. In the fall of 1946 four white birds were utilized for Experiment I, designed to study the orientation of young pigeons in unfamiliar territory. In that experiment, and in the releases

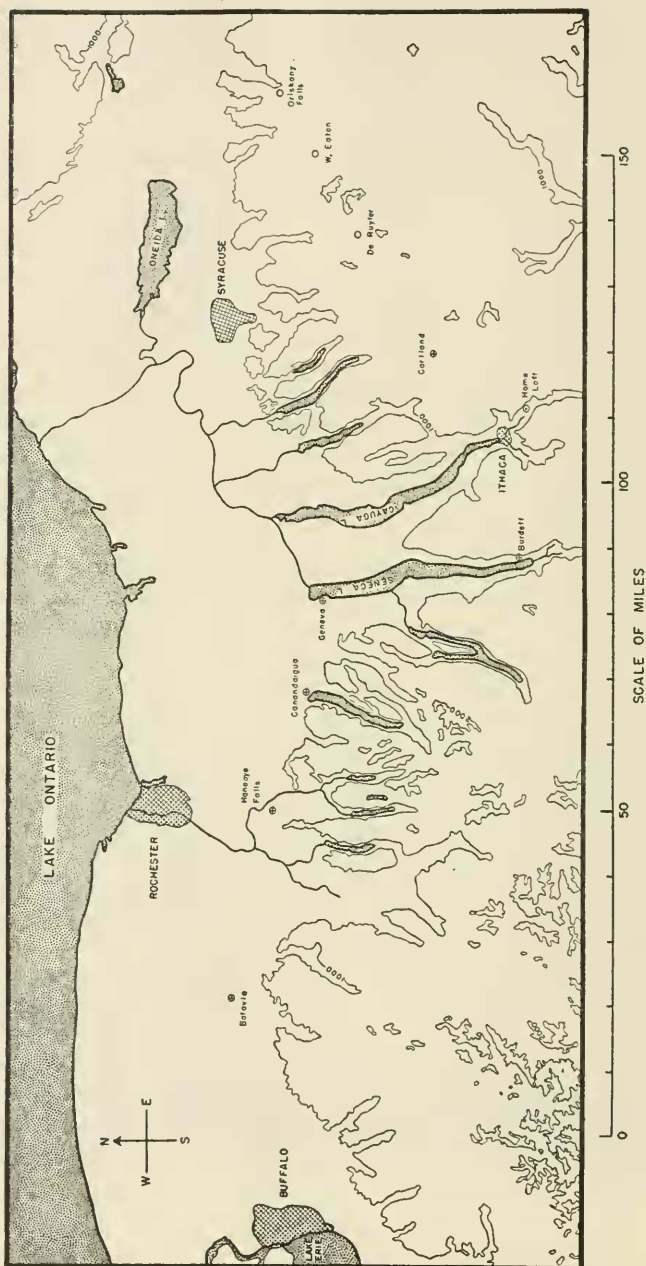


Fig. 1. General area over which the pigeons made their homing flights.

at greater distances during 1947, most of the longer flights were observed from the air, so that at the time of each successive release something would be known of the birds' previous experience and familiar territory.

The general topography of the area in which all of these flights took place is shown in Figure 1; and the details of individual flights are described below, and illustrated in the maps of Figures 2 to 6.

## EXPERIMENT I

### 1. *General plan and preliminary training.*

This experiment employed four white pigeons four to five months old (Nos. 6, 8, 9, and 21); they were first observed during a flight over familiar ground and were then followed from the air as they sought to find their way home from unknown territory. They were given preliminary training by numerous releases in an area extending ten miles northwest, seven miles west, two miles southwest, three miles south, two miles southeast, three miles east, and 21 miles northeast. After one of the later training releases in familiar territory northeast of home, they were followed by airplane. They were next carried 24 miles WNW and released in quite unfamiliar territory where the topography resembled that of a familiar area bordering the south end of Cayuga Lake.

Most of the preliminary training flights were made in the company of other pigeons; but each bird was also released alone on several occasions, so that all had had experience in returning from familiar territory without any possibility of guidance by others of the flock. Nos. 6, 8, and 9 had each completed a total of 39 training flights while No. 21 had made 25. The more distant of these release points employed in the preliminary training are shown in Figure 2 by circles with an enclosed cross. The releases were timed so that the birds never had more than two to three hours of daylight in excess of time required for a direct flight home. If they were back at the loft by nightfall or early the next morning, it was very unlikely that they had wandered to points far removed from the area included in Figure 2.

Two birds, Nos. 6 and 9, never remained away from the loft overnight during this training period, but the other two did have occasional lapses. Number 8 remained out overnight after one release at 7 miles, and after another at 10 miles; after a second release at 7 miles it remained out for two days. Number 21 stayed out overnight

following two releases at 7 and 11 miles, and it remained away from the loft for 36 hours after a release at 8 miles. It was thus possible that these two birds had wandered extensively, and had a large area of familiar territory, although the experience of pigeon racers suggests that such lapses at a relatively early stage in a pigeon's training are caused by preoccupation with rest or feeding rather than extensive wandering. Furthermore, when the group was later released in unfamiliar territory, the bird that exhibited by far the best homing performance was No. 9, which had never remained out overnight, rather than No. 8 or No. 21.

2. *Airplane observation of a flight over familiar territory.*

After the preliminary training outlined above, the four white pigeons were released 11:45 A.M., October 21, 1946, at the Cortland airport and followed during their entire flight to the home loft. As can be seen from Figures 1 and 2, the Cortland airport is 17 miles north-east of the loft. The birds had been released there once before on October 16, and in addition they had been released October 20 at Homer, four miles farther from the loft, so that they had flown over Cortland area on two previous occasions.

After a 10 minute period of circling in the immediate vicinity of the release point (the usual behavior which preceded homing flights by these pigeons), the four birds were joined by a larger flock of local pigeons. Together with these birds they circled over an area south-west of the airport, but finally separated from the local birds and began, about 15 minutes after release, to move along the route shown in Figure 2. During the first five miles they circled continuously, but the trend of their circling was always westward, i.e., slightly to the north of the true course home. When about five miles from the release point their manner of flight changed rather abruptly to straight flight along the course shown. Thereafter their progress was steady with very few sudden turns until they reached their home loft 70 minutes after release. Disregarding preliminary circling, the actual flight path was about 21 miles in length, while the airline distance from release point to home was 17 miles.

3. *Airplane observations in unfamiliar territory with confusing topography.*

The Cortland flight showed that the birds, while neither as fast nor as sure of themselves as highly trained racing pigeons, nevertheless flew an essentially straight course when released in familiar territory.



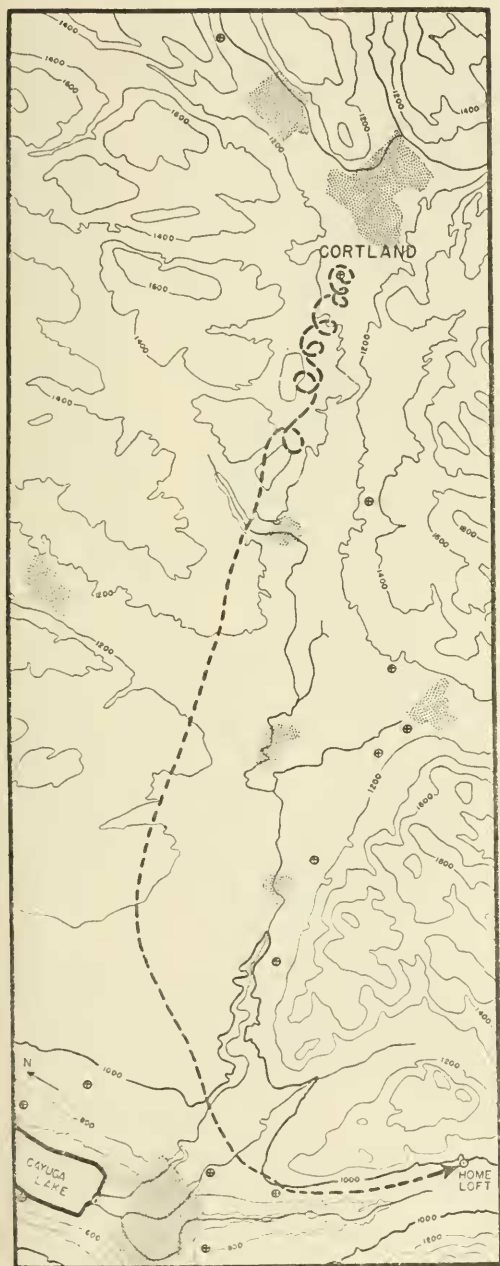


Fig. 2. Route flown by four pigeons over familiar territory in Experiment I. The actual flight path during the first three miles contained even more loops and turns than are indicated. Previous release points are shown on the map by circles with an enclosed cross; note that while the birds flew down the same valley as that traversed during the transportation to earlier release points they did not fly directly past these points.

The next step was to repeat the observation from roughly the same distance into unknown territory. The geography of the Finger Lakes area permitted the addition of a geographical factor which offered some chance of revealing how much the birds depended upon topography. The home loft lay six miles southeast of the southern end of Cayuga Lake, in one of the two well-defined valleys leading south from this end of the lake. Such topographic features, in addition to the presence of the small city of Ithaca at the end of the lake, should be useful for visual orientation of birds released near Ithaca, as these birds had often been. The Finger Lakes are all similar in geological origin and general shape (see Fig. 1); Cayuga and Seneca Lakes have especially similar topography at their southern ends. In both cases there are (1) flat alluvial plains extending one to three miles immediately south of the end of the lake, (2) steep hillsides on both sides of the lake along the southern half of its length, and (3) hills directly south, beyond the alluvial plain, which are divided by two valleys, each containing a small creek. Furthermore, there are cities on both alluvial plains, although these are quite different in appearance. It thus seemed possible that pigeons familiar with the south end of Cayuga Lake might be misled by this similarity when released at the south end of Seneca Lake.

The first release point in unfamiliar territory was therefore placed near Burdett at point A of Figure 3, 23.6 miles WNW from the home loft. This point was analogous to a release point on the eastern shore of Cayuga Lake where the four birds had been released several times during their preliminary training (see Fig. 2). If the pigeons relied upon topography for their orientation, they might be expected to fly south from release point A into the valley leading southeast from Seneca Lake, whereas a true course towards their home would take them ESE. The difference between these two hypothetical courses was about 85 degrees.

The actual release at point A was made at 11:05 A.M., October 27, 1946. In the interval since the flight from Cortland the pigeons had been given two short exercise flights by releases five miles west and 12 miles NNW from the loft. On the 27th they circled for about 15 minutes within a mile of release point A, and then turned abruptly south. The flight south was continued for about  $2\frac{1}{4}$  miles, and at this distance from release point A the birds turned to the east as shown in Figure 2. By this time they were in a region where the topography was clearly different from that of their familiar territory near Ithaca.

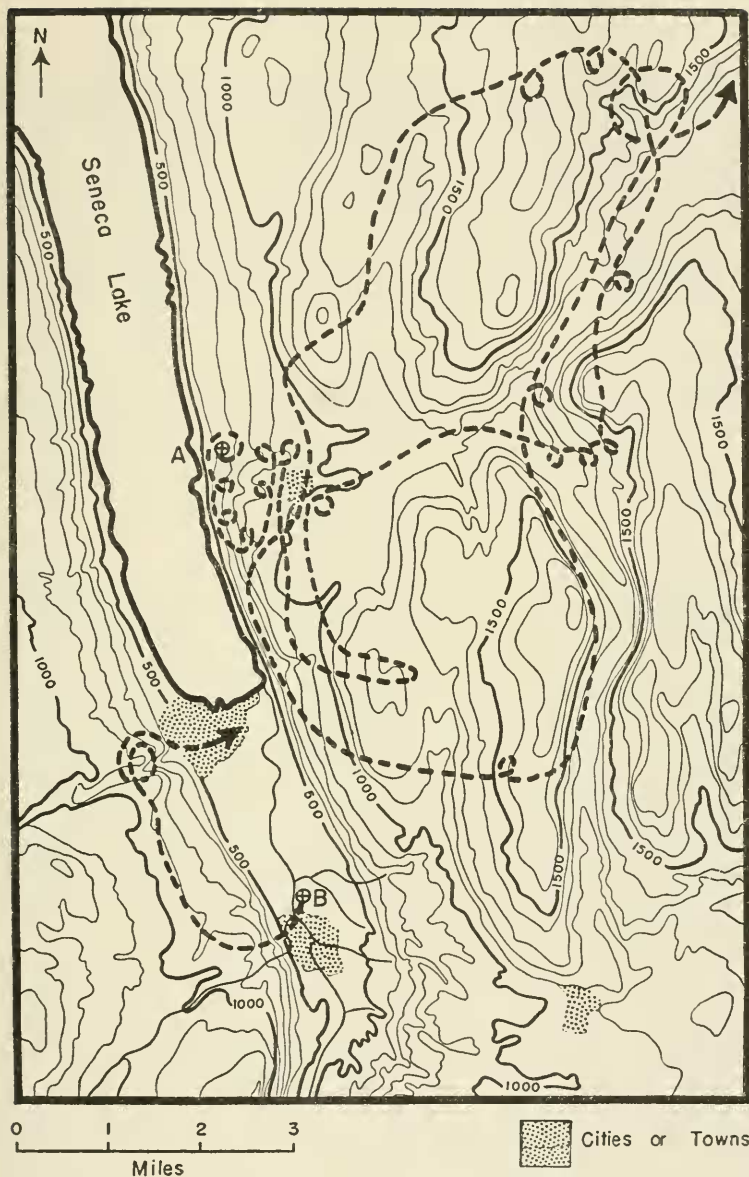


Fig. 3. Route flown over unfamiliar territory by the same four pigeons (as in Fig. 2). Point A was 23.6 miles WNW from the home loft, at a point near the shore of Seneca Lake that was analogous to a previous release point near Cayuga Lake. Note that on two occasions the birds flew south when departing from the vicinity of the release point; this is the direction they would be expected to take if they were misled by the topographical similarity between the two lakes.

After their turn to the east the pigeons returned to Burdett, circled over the village, turned east through a valley and continued along the course shown in Figure 3, which led them back to the vicinity of the release point. Again the birds flew south from Burdett, but this time flew three miles before turning east and then north once more. At one hour and forty minutes low fuel supply forced us to discontinue the observation at a time when the birds were heading northeast. Throughout the period of observation the four birds stayed together, and they flew 35 miles altogether, aside from local circling. Yet at the end of the observation they were only seven miles from the release point, heading  $77^\circ$  north of the correct course towards the home loft. Only one of the four, No. 9, returned to the loft at all, and it required four hours and forty-five minutes for the flight. This should be contrasted with one hour and ten minutes required for the return of the entire group from Cortland over familiar territory.

Pigeon No. 9 was again released at the south end of Seneca Lake (at point B of Fig. 3) at 11:08 A.M., November 9th. The airplane observation of No. 9 on this date was unfortunately terminated after a few minutes, when the pigeon was lost to view against a cluster of white houses in the city of Watkins Glen. But it was back at its loft when I first returned to look for it  $1\frac{1}{2}$  hours later.

The results of Experiment I show clearly that these four young white pigeons were unable to determine the correct direction of their home when released at 23.6 miles in what was evidently unfamiliar territory. The nearest of their previous release points to Seneca Lake was only seven miles from home, so that they had been suddenly carried across 16 miles of hilly territory over which they had no occasion to fly during the preliminary training. The general pattern of their flight suggested that they lacked any clear orientation and conformed to expectations of theories based upon recognition of visual landmarks.

As in most homing flights of pigeons there was a clear separation between the initial period of circling or undirected short flights within a mile or so of the release point, on the one hand, and the rather sudden beginning of a definitely "cross-country" flight which continued in approximately the same direction for a matter of miles. In this case the initial period lasted 15 minutes, and the shift to cross-country flight was abrupt and recognizable at the time it occurred. As noted above, both cross-country flights away from the release point were directed south, just as one would expect if the birds were guided by

the topographical similarity between the southern ends of the Cayuga and Seneca Lake basins. It is not surprising that this topographical delusion failed to persist all the way to a point analogous to the location of the home loft southeast of Cayuga Lake. When the birds had flown south for two to three miles the different appearances of the two lake basins should have become quite obvious; for this flight was largely over open fields, whereas the analogous flight path south from a corresponding point on the shore of Cayuga Lake would have taken the birds over a residential section of Ithaca and over the Cornell campus.

Another not uncommon behavior pattern of inexperienced or disoriented pigeons is to fly for several miles in a closed circuit that returns to the release point after 20 to 30 minutes. This type of flight has been described to me by pigeon racers and, as shown in Figure 3, it occurred after this release of pigeons at point A near Seneca Lake.

## EXPERIMENT II

### 1. *General plan, and previous experience of the birds.*

In the spring of 1947 a flock of 13 experienced pigeons was available, all approximately one year old; seven were white (Nos. 9, 34, 35, 36, 45, 48, and 49), and six were dark colored (Nos. 4, 12, 14, 15, 16, and 17). The previous experience of No. 9 has been described under Experiment I; after the second release near Seneca Lake it had made only short exercise flights and was never out overnight. Nos. 34-49 had been purchased in the fall of 1946 as young birds never flown from their natal lofts; but all of the dark colored birds had been raised at my loft in 1946 and had acquired considerable flying experience. In the course of 26 preliminary training flights from March 23 to May 22, 1947, this flock was brought into good flying condition by releases at several points within an area extending three to five miles east, south and southwest from the loft, 21 miles west, 13 miles northwest, and 5 miles north. In addition Nos. 4, 12, 14, and 15 had made three longer flights during 1946 from release points to the northeast of the loft, all of which are shown in Figure 1. On September 22, 1946, these birds were released at DeRuyter, N. Y., 42 miles northeast, at 3:45 P.M.; all were back at the loft by 6:30 P.M. On September 26 they were released at West Eaton, N. Y., 52 miles northeast, at 4:15 P.M.; three were again back by nightfall and the fourth, No. 12, was home by 7:30 A.M. the following morning. The

longest of these flights was made October 4, when three of the birds, Nos. 4, 14, and 15 were released at 1:00 P.M. near Oriskany Falls, 65 miles northeast of their home loft. Nos. 14 and 15 reached the home loft at 4:26 P.M., but No. 4 did not return until sometime between 5 P.M. October 5 and 9:00 A.M. October 6. Thus all flights except the return of No. 4 from Oriskany Falls occurred with sufficient speed to assure that no extensive wandering from the direct course home could have taken place.

In Table 1, I have summarized the previous experience of the 13 pigeons used for Experiment II, together with the most serious cases where their return was slow enough to allow for possible wandering into the area of later releases. In each case the instance of slow homing listed was the worst one in the bird's record, and none of its other lapses could have significantly increased the probability that the later release points of Experiment II had been visited. In Table 1, the homing times refer to the time when the bird was actually seen at the loft; in some cases a day or two elapsed between complete checks, so that some of these pigeons probably returned considerably sooner than indicated in the table.

The general plan of Experiment II was to release the flock at progressively greater distances northwest from Ithaca, following the birds from the air after each release in unfamiliar territory. Because of occasional slow returns before the final releases at 55 miles or more, it is not possible to establish with complete certainty that any individual release was made in what was unfamiliar territory for every bird in the flock. But the probability that *all* of the more distant release points had been visited previously appears extremely small, and the results as a whole cannot reasonably be explained as orientation based exclusively upon familiar landmarks and exploration. The routes flown by various birds are presented in Figures 4, 5, and 6, and the pertinent observations on individual behavior are contained in a condensed summary of each observation. It was unfortunately not possible to provide a continuous watch for returning birds at the loft; but unless stated otherwise, all of the birds returned soon enough after release to establish the fact that they had flown home without extensive detours.

## 2. *Description of individual flights.*

*Covert*, 19 miles northwest; birds released 12:35 P.M., May 24, sky almost fully overcast, warm, hazy, visibility five miles, calm. The flock circled within half a mile for 10 minutes, then in larger circles tending more to the south

TABLE I. Previous history of pigeons used in Experiment II, and their homing performance during the experiment. An asterisk, \*, indicates a sufficiently early return to show nearly straight flight home; in all other cases the maximum homing time is given. Parentheses, ( ), indicate that the bird was not flown.

Pigeon number	4	12	14	15	16	17	9	34	35	36	45	48	49
Color	blue bar	blue check	blue bar	blue bar	blue bar	red	white	white	white	white	white	white	white
Longest flight in 1946	65 m. NE.	52 m. NE.	65 m. NE.	65 m. NE.	( )	22 m. NE.	24 m. WNW.	( )	( )	( )	( )	( )	( )
Slowest previous homing flight	41 hrs. at 65 m. NE. (1946)	48 hrs. at 21 m. NE. (1947)	always a good homer	over-nicht at 11 m. in 1946	5 days (first flight, 1946)	5 days (first flight, 1946)	always a good homer	always a good homer	overnight at 15 m.	48 hrs. at 21 m. WSW.	48 hrs. at 21 m. WSW.	several days at 4 m.	4 days at 21 m. WSW.
Covert May 24, 12:35 P.M.	*	*	*	*	*	*	*	*	*	*	*	*	( )
Interlaken May 26, 3:07 P.M.	*	24 hrs.	*	*	2 days	*	*	*	2 days	24 hrs.	*	24 hrs.	( )
Covert May 31, 3:25 P.M.	*	*	*	*	*	*	*	*	( )	( )	*	*	*
Interlaken June 1, 2:30 P.M.	*	*	*	*	*	*	*	*	*	*	*	*	*
Scott's Corner June 10, 3:27 P.M.	overnight	*	overnight	*	overnight	*	*	overnight	overnight	overnight	*	overnight	*
Willard June 13, 1:23 P.M.	*	*	*	*	*	*	*	Newark June 16	*	*	lost.	lost.	*
W. Fayette July 15, 11:25 A.M.	2 days	*	Riehlard July 21	*	*	*	*	lost	2 days	*	lost on exercise flight	lost on exercise flight	7 days
Geneva July 23, 3:01 P.M.	*	*	*	*	4 days	*	*	*	*	*	*	*	*
Canandaigua July 25, 2:42 P.M.	*	*	*	*	( )	*	*	*	lost	*	*	*	*
Interlaken Sept. 23, 3:35 P.M.	*	*	*	*	1-4 days	*	22 hrs.	*	22 hrs.	22 hrs.	*	*	1-4 days
Ovid Sept. 27, 9:50 A.M.	*	*	*	*	*	*	*	*	*	*	*	*	*
Geneva Oct. 2, 2:53 P.M.	*	*	*	*	*	*	*	*	*	*	*	*	*
Canandaigua Oct. 7, 2:15 & 4:15 P.M.	*	*	*	*	*	*	*	*	*	*	Webster Oct. 11	*	lost
Honey Falls Oct. 12, 11:02 A.M.	20-24 hrs.	lost	lost	lost	killed near Tru-mansburg	lost	20-24 hrs.						
Batavia Oct. 21, 1:40 P.M.	lost	lost	lost	lost	lost	lost	lost	lost					

and east than north and west. Four or five times they returned to the release point. At 20 to 25 minutes they came within sight of Cayuga Lake and suddenly turned towards its shore (see Fig. 4). On reaching the lake they flew south along the shore until at four miles north of Ithaca they crossed the lake and continued south along the east shore and thence directly home to reach the loft 55 minutes after release.

*Interlaken*, 22 miles northwest; birds released 3:07 P.M., May 26; clear, visibility unlimited, polar continental air mass, wind southwest, moderate, sharp updrafts, cumulus clouds forming by the end of observation. The birds circled within 0.3 mile for 13 minutes, then flew east or ESE to reach Cayuga Lake (which was visible from the release point) at about the same point as on May 24. They then flew south along the west shore of the lake as shown in Figure 3 and were lost to view over Ithaca. Numbers 12, 36, and 48 were out overnight, and Nos. 16 and 35 did not return until two days after release.

*Covert*, 19 miles northwest; birds released 3:25 P.M., May 31. They were not followed by air, but were observed from the ground to fly off to the west, return ten minutes later to the release point, and then head south.

*Interlaken*, 22 miles northwest; birds released 2:30 P.M., June 1; solid overcast, visibility eight to ten miles, gentle SSE wind, light rain just before and after flight. The birds circled 15 minutes, mostly to the south, then headed east. Two miles from release point the flock split; one group continued southeast and another, which I followed because it contained three white birds, continued SSE along the main highway, thus passing close to all of the previous release points (see Fig. 4). In fact, they seemed to seek out these spots, flying within 200 to 300 yards of each previous release point and circling over the one at Trumansburg, although at other times they deviated a quarter to a half mile from the highway.

*Scott's Corner*, 25 miles northwest; birds released 3:27 P.M., June 10; clear, warm, slight haze, visibility eight miles, a few cumulus clouds forming, light south wind. The birds circled near the release point for 17 minutes, flying more often to the south and east than in other directions. They then flew ESE with some veering, reached Cayuga Lake near Shelldrake Point, and turned south along the lake shore after first flying 200 yards out over the water (see Fig. 4). Fifty-eight minutes after release the flock under observation contained five white and three dark birds, and these eight landed on the shore of the lake near Jacksonville so that they could not be followed farther from the air. Numbers 4, 14, 16, 34, 35, 36, and 48 remained out overnight; that is, three dark and four white birds. This is only one bird less than the number seen to land, so that it seems likely that other activities than wide wandering caused this slow homing.

Up to June 10 the birds were given every opportunity to learn the topography and landmarks. They were carried to the release points in a cage attached to the roof of an automobile and not only was each release point within sight of the previous one from an altitude of 100 to 200 feet, but all were within two



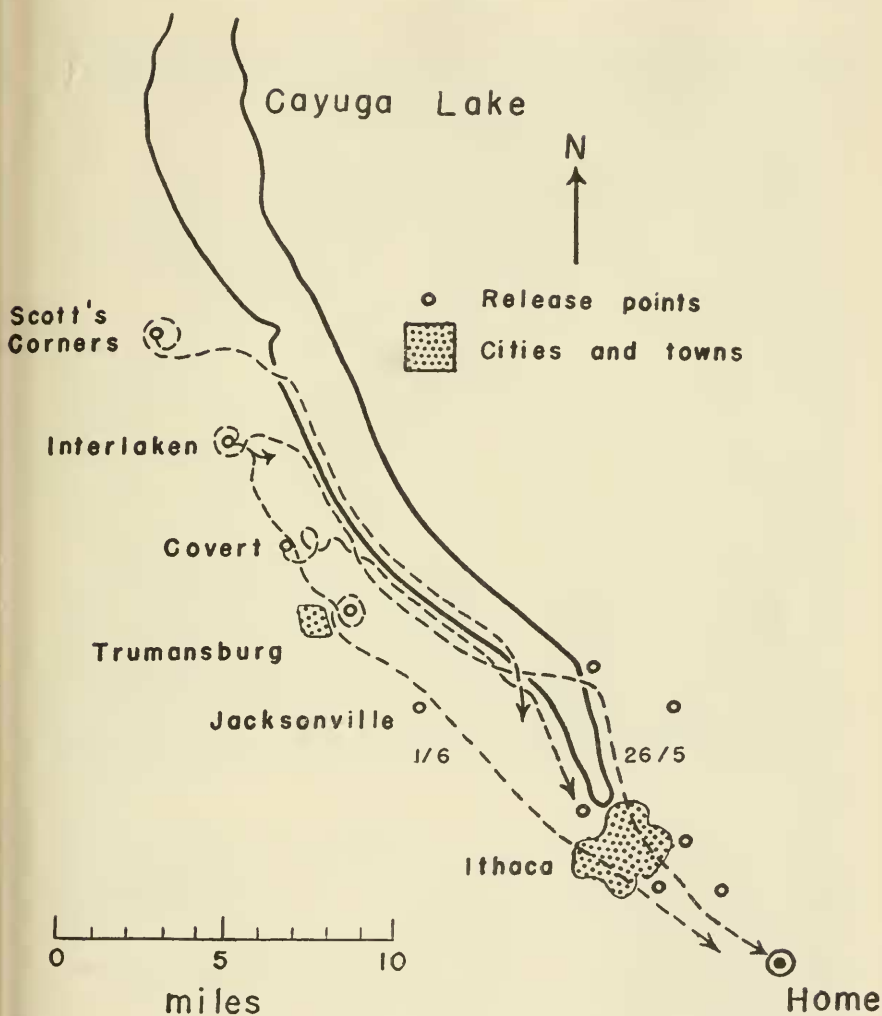


Fig. 4. Routes flown by pigeons during the early stages of Experiment II; all these release points were within a mile or two of familiar territory. Note that after the release at Interlaken on June 1 the birds that were being followed flew directly over several of the previous release points.

miles of Cayuga Lake. The birds returned in all observed cases by following the shore line of the lake, or in one case by flying along the highway leading past all of the previous release points. After June 10, however, the birds were carried in closed boxes inside the automobile or airplane and were taken to release points separated by greater distances. Table 1 shows that the losses increased sharply when these changes were made. Clearly the releases after June 10 provided a more strenuous test of the pigeons' homing ability.

*Willard*, 32 miles northwest; birds released 1:23 p.m., June 13, partly overcast, moderate south wind, visibility about 15 miles, moderately bumpy air with high stratus and stratocumulus clouds. This release provided an opportunity to test the influence of topography, for the birds had previously been released close to Cayuga Lake (Fig. 4) and on reaching it had only to turn right and follow the shoreline in order to reach Ithaca. At Willard, however, they were released about  $1\frac{1}{2}$  miles from Seneca Lake as shown in Figure 5. If they relied upon simple topographical orientation one would expect them to circle, notice Seneca Lake, fly to it, turn right along its shore, and head north — almost directly away from home. The birds circled for only about five minutes, then flew southwest and reached the shore of Seneca Lake at ten minutes. So far they had behaved roughly as would be expected on the basis of the topography. On reaching the lake, however, the flock turned south, flew inland about one-half mile to a railroad track along which they continued southward. About one mile south of the village of Willard the flock split, four white birds continuing south, and others turning back to the north. There were at least two white birds in the latter group, and almost certainly they were Nos. 34 and 45 which failed to find their way home. One of these, No. 34, was picked up at Newark, N. Y., on June 16, and later returned to me. Newark lies 28 miles NNW from Willard (see Fig. 5) and it seems quite possible that these two white birds broke away from the flock because they were indeed misled by the topographic resemblance to previous release points near Cayuga Lake.

The group which continued south, containing four white birds, flew a surprisingly straight course towards home, as shown in Figure 5, despite the fact that this course led them over many miles of territory never previously visited when under observation. But some of these pigeons might have visited the Willard area during one of the longer periods away from home after an earlier release (for example, No. 35 had been out for two days after the release at Scotts' Corner, and Nos. 12, 16, 21, and 45 may have been out as long as 48 hours after a release 21 miles WSW of the loft).

After reaching the city of Ithaca the group made a detour across the valley extending southwest from the end of the lake, instead of flying southeast to their home loft. This detour inside of very familiar territory is difficult to understand; it should be compared with another detour within familiar territory that occurred on July 25 after the first release at Canandaigua.

*West Fayette*, 38 miles northwest; birds released 11:25 a.m., June 15; high

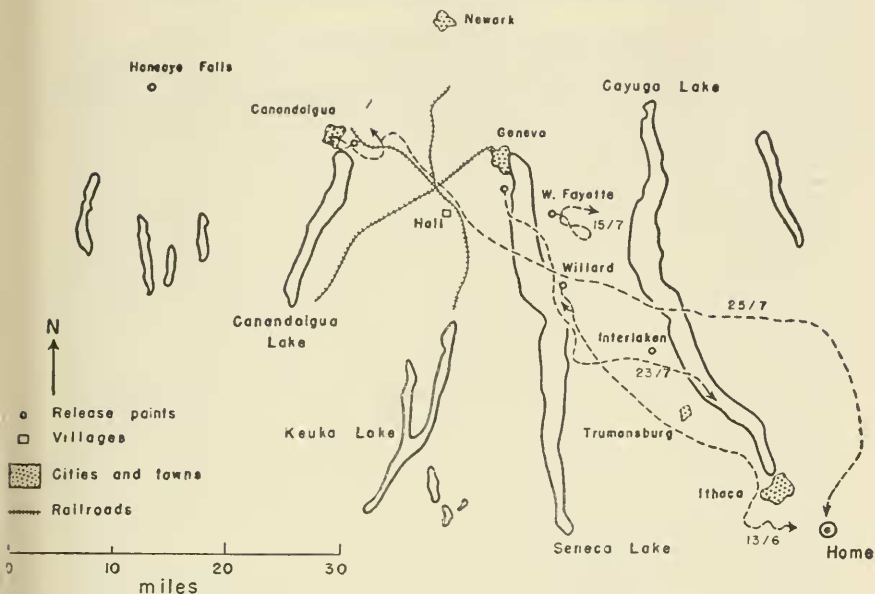


Fig. 5. Routes flown in Experiment II after releases at 32 to 55 miles from home, in what was probably unfamiliar territory. Note the generally correct direction taken in most instances. The observed flight path of No. 34 after its release at Willard is indicated by the small arrow branching away from the path taken by the main flock; this bird was recovered at Newark, and may have been misled by the lake topography. Note also the case of an apparent "overshoot" across familiar territory after the release at Canandaigua on July 25.

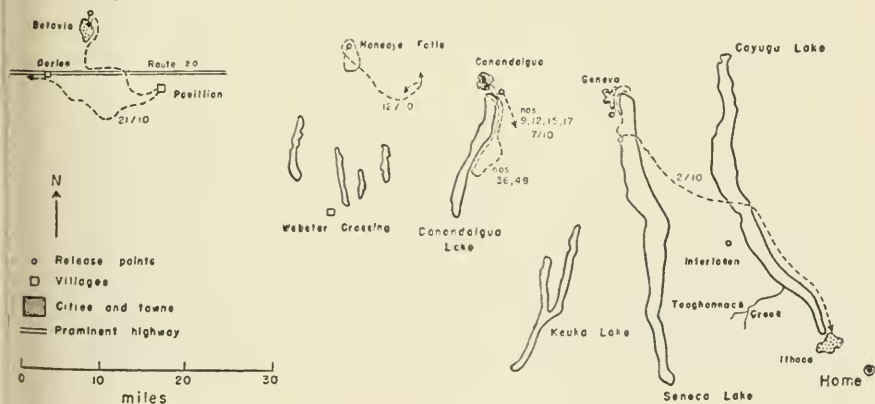


Fig. 6. Routes flown after the second releases at Geneva and Canandaigua, and after the final releases at Honeoye Falls and Batavia in what was almost certainly unfamiliar territory. Note the nearly correct initial flight direction in all cases.

solid overcast with lower cumulus clouds at 2500 feet, scattered showers, hazy, visibility 4 to 5 miles, moderate SSE wind. These were the most adverse weather conditions, and also the poorest visibility, of any release involving airplane observation. The birds circled for 20 minutes, then started southeast as shown in Figure 5, but after  $1\frac{1}{2}$  minutes turned east and flew to within three miles of Cayuga Lake (which, however, was not visible). There they turned south, and then back to the west, next northwest, and finally returned to the release point 35 minutes after they had been set free. They next flew ENE and east and were finally lost to view 55 minutes after release. Pigeon No. 34 was released separately from the other birds in order to see whether its wanderings between Willard and Newark had had any effect. It was not followed from the air, but it headed west from the release point and never returned. The main group also did poorly. The first birds returned after six hours, and No. 14, which had previously appeared to be one of the best fliers, was found six days after release at Richland, N. Y. — 68 miles northeast of the release point. Numbers 4 and 35 were out for two days and No. 49 was not back until a week after release. Here was striking confirmation of the pigeon racers' experience that weather involving very poor visibility has an adverse effect on pigeons' homing performance.

*Geneva*, 43 miles northwest; birds released 3:01 P.M., July 23; almost solid overcast at 5000 to 6000 feet and half coverage of cumulus clouds at about 3000 feet, strong updrafts, wind generally west. The birds circled near the release point for 17 minutes, with two false starts to the south along the shore of Seneca Lake; after each of these southward flights they returned to the release point. They next flew south for two miles, turned sharply east across the lake, and turned south again along its eastern shore as shown in Figure 5. This portion of the flight crossed terrain over which they had flown on June 13, but now they continued south along the lake shore about two miles farther than on the 13th. There the flock split, and we followed two white birds which flew straight east along a road which led them into Interlaken. Next they flew southeast to Cayuga Lake and continued home along its west shore just as they had done on so many previous flights. Number 16 remained out for 4 days after this release.

*Canandaigua*, 55 miles northwest; birds released 2:42 P.M., July 25; four-tenths coverage with cumulus clouds, visibility eight to ten miles, modified polar continental air mass, warm, light westerly winds with surprisingly smooth air. This release represented the longest step yet taken into presumably unfamiliar territory. The birds circled the release point for 23 minutes, including a flight one mile to the south; but they returned frequently to the release point. They then flew west over the city of Canandaigua, returned once again to the release point, and next headed ESE along the route shown in Figure 5. When the main flock made a turn to the north one white bird separated from the rest by turning farther and heading northwest. The main group flew along a railroad for some distance as shown in Figure 5, and after

reaching Seneca Lake followed roughly the same route as that flown from Geneva to the west shore of Cayuga Lake on July 23. Here, however, they surprised us by continuing directly east across Cayuga Lake and holding to the same direction for 15 miles more. As shown in Figure 5, they eventually turned south and reached territory which must have been familiar from flights made in 1946. It is even possible that the whole area ten to fifteen miles east of Cayuga Lake had been visited by one of the birds either in 1946 when returning from releases up to 65 miles northeast, or during the long period required to return from the West Fayette releases on July 15. But why these birds flew so far east of Cayuga Lake is difficult to explain, for they were already at the shoreline along which they had flown home on previous occasions. The whole performance is reminiscent of pigeon racers' description of an "overshoot". This is reputed to be a flight in which pigeons continue flying in the same direction, passing their own loft and landing at some other loft in the same city which lies farther from the release point than their own home. Number 35 was lost on this flight, and it may well have been the single white bird that broke away to the northwest shortly after the flock left the vicinity of Canandaigua.

After this 12-mile step into presumably unfamiliar territory, the birds took essentially the correct direction, except for short flights near the release point, just as they had done at Willard. It is far less likely that they could have found familiar landmarks near Canandaigua, however, for no exploratory flights west of Geneva had been observed. Nevertheless, there had been opportunity for wandering into the Canandaigua area after the release at West Fayette, when Nos. 4 and 35 were out for two days and No. 49 may have been out for as long as seven days, and also after the release at Geneva, when No. 16 may have been out as long as four days.

During August it was not possible to make further observations of these pigeons. They were given two short practice flights from Interlaken (3:35 P.M., September 23) and Ovid (9:50 A.M., September 27); on the first flight, No. 9 stayed out overnight and Nos. 16 and 49 remained away from the loft for four days. Evidently their homing ability, or more likely their physical stamina for long flights, had been impaired by two months with no activity except exercise flights in the immediate vicinity of the loft.

*Geneva*, 43 miles northwest; birds released 2:53 P.M., October 2; high broken altocumulus clouds and occasional sunshine, visibility 10 to 12 miles with patches of haze, wind northwest 10-12 mph at the outset but dropping to five mph at the end of the observations. The birds circled for twenty minutes at the release point, making during that period two flights of one half mile to the south and back to the release point. They next flew north over the city of Geneva, returned once again to the release point, and finally headed south along the route shown in Figure 6. During the ensuing southward flight along the lake shore they twice flew out over the water for 200 to 300 yards and then returned to the land. It was tempting to infer that two dark birds which

in each case flew farther from land than the rest were attempting to lead the flock across the lake. The flock did turn sharply to the east and crossed Seneca Lake only when it arrived at the point where the birds had reached the lake on their flight from Canandaigua on July 25. The remainder of this flight followed routes flown on previous occasions.

*Canandaigua*, 55 miles northwest; birds released October 7; clear, hot, visibility 15 miles with slight haze in patches, gentle southwest winds. The flock was divided into two groups; the first group to be released (Nos. 4, 16, 36, and 49) were carried from Geneva to Canandaigua at the window of the airplane in an attempt to "show" them the terrain. After being set free at 2:15 P.M. these four birds interrupted their initial circling near the release point by a sojourn on the roof of a barn and silo in the company of local pigeons; but at 30 minutes after release the four birds circled several times over the city of Canandaigua and the north end of Canandaigua Lake. At this time the two white birds separated from the others and were followed south along the route shown in Figure 6. After another return to the release point at 68 minutes after release these two white birds spent another 20 minutes over the city of Canandaigua before being lost. Neither returned to the loft; but one, No. 36, was reported from Webster, N. Y., 25 miles southwest from Canandaigua, between October 11 and 13. Evidently the previous flight from Canandaigua three months before, together with the view of the landscape from the airplane window, had not sufficed to permit successful orientation by visual landmarks. Numbers 4 and 16 found their way home, but No. 16 remained out overnight.

The remaining four birds flew SSE immediately after release at 4:15 P.M. with no circling at all, but were unfortunately lost to view six miles SSE from the release point when they apparently landed in a patch of woods (see Fig. 6). This relatively straight flight departed almost immediately from the area over which these birds had flown after their previous release at Canandaigua on July 25. Three birds of this group homed promptly, but No. 17 remained out overnight.

*Honeoye Falls*, 72 miles WNW; birds released 11:02 A.M., October 12; clear and warm, visibility eight to ten miles with slight haze, wind SSW eight to ten mph. The birds circled near the release point for 13 minutes before flying the route shown in Figure 6. Their first heading was south for four miles, but they then turned east and circled back to the release point 23 minutes after release. On their second departure to the southeast they flew considerably farther. The lone white bird, No. 9, separated from the others at the point indicated on the map and could not be followed farther. The returns from this release were very poor; three birds with excellent previous records were never heard from again (Nos. 12, 15, and 17), and the two which did return (Nos. 4 and 9) arrived somewhere between 20 and 24.5 hours after release. The remaining bird, No. 16, was reported found dead near Trumansburg on October 25 (apparently shot). It was thus close to the direct line between the release

point and home (see Fig. 4).

Despite the heavy losses, it was clear that the flock followed from the air did set out in nearly the correct direction while still within two miles of the Honeoye Falls release point. The only slow returns on previous flights had occurred after releases at Interlaken, West Fayette, and Geneva, 29 to 50 miles east of Honeoye Falls. It is surely difficult to believe that even one bird had wandered by chance to the immediate vicinity of this release point at Honeoye Falls, so that the flock must have been able to select the approximate direction of home without benefit of visual landmarks.

*Batavia*, 100 miles WNW; birds released 1:40 P.M., October 23; clear and warm, haze in patches caused visibility to vary from four to nine miles, wind WNW, light. The birds circled for five minutes, landed in a tree near the release point for five minutes more, and then flew rather directly south along the road leading into the city of Batavia. They circled over the city and returned to the release point. They then separated, so that only the white bird, No. 9, could be followed as it circled back to the south and continued southeast along the course shown in Figure 6. The sharp turn to the east occurred as it reached a prominent four-lane highway, along which it flew for about three miles. At Pavillion it landed on a housetop and remained for the period from 78 to 117 minutes after the time of release. During this interval the visibility increased considerably as a patch of haze over Pavillion moved to the east. After leaving Pavillion along the route shown on the map, No. 9 headed in a generally westerly direction and at 168 minutes after release it again came to the same highway near Darien. Once more it turned left and flew along this highway until lost to view among a large flock of local pigeons which it joined approximately three hours after its release at Batavia.

The flight of No. 9 was the longest traced from the air, covering 54 miles during the 2¼ hours of actual cross-country flight. Despite this bird's success in all previous flights it seemed lost and disoriented towards the end of the period of observation. Yet it can be seen from Figure 6 that even in this flight the first hour constituted progress in a generally correct direction. Both birds in this final experiment had returned from Honeoye Falls in 20 to 24.5 hours, of which only between 9 and 14 hours were daylight, so that the chance of their having acquired a familiarity with the vicinity of Batavia is very remote indeed. Once again it is necessary to conclude that these pigeons could select the correct direction without reliance upon visual landmarks.

## DISCUSSION

An experienced pigeon racer would immediately recognize from these case histories that my pigeons, especially the white birds, did not display the same physical stamina for long flights as his successful racers. The losses became serious at shorter distances than in the training of the best strains of racing pigeons, and the several occasions

when the birds landed showed that they were not racing for home. It should be recalled, however, that my birds were intentionally deprived of the company of more experienced pigeons on any of their training flights. In most pigeon races, birds of widely differing experience, and from several lofts, are released together.

Some of the present observations indicated a tendency for the birds to follow linear landmarks such as railroads, prominent highways, and the shores of the Finger Lakes. In the releases at Willard and Burdett topographic factors seem to have led certain birds astray. Most striking, however, was the tendency for the birds to fly rather straight courses for several miles in a generally correct direction. On several occasions, as noted above, this occurred in territory where the birds had never previously been observed to fly. The "overshoot" after the first Canandaigua release is especially interesting in view of pigeon racers' reports of similar occurrences.

To explain the essentially correct direction taken in several cases one might assume that the birds had actually visited the release area after some previous release, during the excess time above that required for a direct flight home. The releases at Honeoye Falls and Batavia are good examples; for the flock took the correct initial direction within two miles of the release point. Individual birds had remained out for one to four days after releases at Interlaken, West Fayette, or Geneva. But it seems improbable that they had indulged in enough wandering to have carried them over the area immediately surrounding Honeoye Falls or Batavia. Moreover the birds often deserted the correct direction after about an hour of flying; if they were indeed familiar with the countryside one would not expect this to occur.

It should be borne in mind that all of the more distant release points in Experiment II lay nearly on a line extending approximately northwest from the home loft. The birds flew in a generally southeasterly direction after release in what was almost certainly unfamiliar territory. This could be considered either as an ability to fly towards home, or alternately as an ability to fly southeast, learned in the course of several previous flights in that direction. The obvious critical experiment of a release at 75 to 100 miles in some totally different direction was planned, but could not be carried out because of the rapid dwindling of the flock.

The possibility that the sun is used as a means of orientation by birds should not be overlooked; such a notion has become more attractive in recent years because of the remarkable discoveries of von



Frisch (1950) concerning the precise orientation of insects with reference to the sun. The results of the release at West Fayette coincide with racers' experience that heavy losses are likely to occur in the presence of a heavy overcast and poor visibility. It should also be recalled that in pigeon races of 100 miles or more it is customary to make all releases in the early morning, and furthermore to select release points at various distances so that they all lie in roughly the same direction from the home lofts. Such arrangements might possibly have been adopted empirically because they facilitated an initial orientation relative to the rising sun. In Experiment II the releases were made in the middle of day, with one or two exceptions. It had been my original plan to vary the hour of release in order to test the possibility that the sun's position was an important factor, but the heavy losses at distances beyond 50 miles made this impossible.

The relatively slight variation in time of day at which pigeons were released did not appear to be correlated with the direction of their flight except in one case. In the second release at Canandaigua on October 7, 1947, the flock of eight birds was divided into two groups of four, and the second group to be released had been held in their shipping box for somewhat longer than was usual in these experiments. The behavior of this group after release was striking in that they began a cross-country type of flight almost immediately after their release without the ten to twenty minutes of circling in the immediate vicinity of the release point that occurred in almost every other case. The hour of this release, 4:15 P.M., was distinctly later than that of any previous release at more than 20 miles (for example, the five preceding releases had been at 2:53 P.M., October 2; 9:50 A.M., September 27; 3:35 P.M., July 25; 3:01 P.M., July 23; and 11:25 A.M., July 15). The approximate heading of the pigeons during this straight flight observed from the air between 4:15 and 4:30 P.M., October 7, was  $160^{\circ}$ ; this may be compared with a heading of  $135^{\circ}$  flown by the flock followed after a previous release at Canandaigua on July 25, after the birds had begun an essentially straight flight over what was probably unfamiliar territory. This shift of about  $25^{\circ}$  to the south corresponds to the sun's movement across the sky in one hour and forty minutes, a rough agreement with the time interval separating this release from the customary release time between 2 and 3 P.M. This single correlation can, however, be considered merely as a suggestive indication.

Subsequent to these observations four additional studies of pigeon

homing have been reported. Hitchcock (1950, 1952) has followed flocks of U. S. Signal Corps racing pigeons or their immediate progeny over both familiar and unfamiliar territory. The greatest distance of transportation from the home loft was 190 miles. Hitchcock observed many deviations from the direct course home while following these pigeons from small airplanes — even within familiar territory. The control of previous flights was apparently less complete than in the experiments reported above, so that it is more difficult to set precise limits to the birds' familiar territory. But in three significant cases birds trained to return to their home loft in New Jersey from release points up to 100 miles to the west were carried 100 to 190 miles north and followed after release in what was certainly unfamiliar territory. In all three cases many birds headed to the east or southeast for the first 25 to 50 miles, demonstrating a tendency to take the direction of the previous training flights even though this direction led them away from home.

On the other hand, in these and other flights observed by Hitchcock some birds were clearly able to head towards home even from unfamiliar territory. In the clearest case birds were first trained by releases up to 35 miles to the northwest, 17 miles to the east, 28 miles to the southwest and 87 miles to the southeast. They were then released at Massena, N. Y., 106 miles northwest of the home loft at Middlebury, Vermont. These birds were followed over a route reminiscent of the flight paths described above at Honeoye Falls and Batavia. The general trend of the flight path clearly lay between east and south, so that these pigeons were taking the correct general direction. There was, however, one complicating geographical factor in the Massena experiment. Virtually all the previous flights of these pigeons had been in hilly or mountainous regions of Vermont or the Adirondack area of New York. Massena lies in the broad, flat valley of the St. Lawrence River, and at the time the birds were observed the Adirondack mountains were apparently visible. Hence the pigeons might possibly have been using these mountains as an ecological cue (in the meaning discussed earlier, Griffin 1944); but in view of other evidence discussed below it seems far more likely that these pigeons were in fact able to select roughly the correct direction in unfamiliar territory.

Yeagley (1947 and 1951) has reported extensive experiments with homing pigeons designed to test a theory of bird navigation based upon an assumed sensitivity to terrestrial magnetism and to the Coriolis force. This theory has been adequately and severely criticised

from several points of view (Thorpe 1949); but some of Yeagley's recent work has involved airplane observations of pigeons, both in familiar and unfamiliar territory. Again the pigeons sometimes showed wide deviations from the direct course, even within familiar territory. Fourteen birds were followed for significant distances after individual releases in totally unfamiliar territory (several hundred miles from home); thirteen of these were released at the same point and one at another point several miles to the north. Nine of the first 13 birds flew in a northwesterly direction, while the remaining four scattered in other directions. The single bird set free at a different release point also flew to the northwest. It is difficult to accept Yeagley's explanation of these flight paths for reasons made clear by Thorpe and other critics; and there does not seem to have been any clear relation between the northwesterly heading and previous training flights. The selection of the same general direction of flight by so large a proportion of these birds complements the evidence discussed above for some orienting factor that is related to *direction*, rather than to *position* of the home loft.

A third recent contribution by Kramer and his associates (Kramer and St. Paul, 1950; Kramer and Seilkopf, 1950; and Dinnendahl and Kramer, 1950) offers further support for this point of view. Pigeons released in unfamiliar territory, at some distance from the line along which previous training releases had been made, tended to start their flights in the direction of the earlier training flights; and they required longer, on the average, to reach their home than when released along the line connecting the previous release points with the home loft.

All this evidence, together with Skinner's recent demonstration (1950) of the striking ability of pigeons to retain visual memories of landmarks, suggests that orientation is based upon visual factors, but not solely upon topographic memory of familiar territory.

Matthews (1951) has recently presented a substantial contribution to the problem of pigeon navigation. Using birds raised especially for his experiments by experienced and successful racers he judged their homing performance both by the customary standards of speed and percentages of returns and also by the initial direction of flight observed through binoculars from the release point. In his earlier experiments with birds of three to four months trained up to distances of 18 miles, and trained predominantly in one direction, Matthews found that releases in unfamiliar territory tended clearly to result in flights that approximated the training direction. In this the results were

similar to those reported by Kramer *et al.* and by Hitchcock. But in Matthews' later experiments with more experienced birds (training flights of 25 to 127 miles) the initial flight directions after release in unfamiliar territory centered around the true direction of home rather than approximating the training direction or scattering at random.

Matthews showed, by releases at different times of the day, that no simple insect-like flight at a fixed angle to the sun could account for even those cases where birds in unfamiliar territory did hold to the direction of their training flights. In other experiments he obtained entirely negative results from a repetition of Yeagley's experiments in which magnets attached to homing pigeons were reported to worsen their homing performance. Matthews found that on the average the homing performance of his birds was better on clear or partly cloudy days than under a solid overcast, and he is inclined towards some explanation of pigeon navigation based upon the position of the sun.

Taking all of these results into consideration we may conclude that pigeons vary so greatly in homing ability that it is advisable to distinguish three distinct levels of navigational ability. What we may conveniently call type I homing is reliance upon "contact flying" within familiar territory. When released in totally unfamiliar territory birds which exhibit only type I homing show a quantitative homing performance that can easily be accounted for by theories of exploration or even by a completely random search for familiar landmarks. They may be misled by topographic features resembling portions of their familiar territory. Clear examples would be the pigeons of Experiment I. Pigeon racers generally believe that young and inexperienced pigeons home in this way, and, among wild birds, the gannets followed by airplane gave every evidence of employing type I homing.

A second level of homing, conveniently designated type II, is the ability to maintain flight in roughly a fixed *direction*, usually that adhered to in previous training flights. Examples would be the birds from Fort Monmouth, New Jersey, followed by Hitchcock after being released in central New York State; these birds had been trained to fly east from training releases in Pennsylvania, and they were followed by air as they flew easterly courses over unfamiliar territory. The earlier experiments of Matthews and the behavior of pigeons described above after releases at Canandaigua, Honeoye Falls, and Batavia appear to be type II. Since most pigeon races involve a series of release points all lying in roughly the same direction from home, flying in a fixed direction may be of predominant importance in pigeon

racing. Furthermore the results obtained with wild birds by Schüz (1934, 1949), by Rüppell (1944) and by Rowan (1946) suggest that cross-country flights in roughly a fixed direction may be of importance in the natural migrations of many wild birds.

Finally there is a third level of homing ability, conveniently designated as type III, which permits birds to fly approximately straight towards home from unknown territory *regardless of the direction in which home lies*. Such an ability has long been tacitly assigned to homing pigeons and to wild birds; but aside from unsatisfying, indirect evidence such as that obtained with petrels (Griffin, 1940), the recent work of Matthews with pigeons affords the first rigorous evidence for the existence of this third and most remarkable type of homing. In addition, at least one of the pigeon flights traced from the air by Hitchcock appears to fall into type III. Most recently of all, Kramer and von St. Paul (1952) have reported two additional cases of type III homing in pigeons.

In differentiating between these three types of homing one must not forget that the same flock of pigeons may exhibit two, or even all three, of these types of orientation at different times during a single homing flight. Thus Hitchcock's birds which had been trained to fly east and were then released in unfamiliar territory did follow an easterly course that continued for an hour or two. But then they shifted to a different, and usually a more correct, direction, perhaps because the flight in the direction of previous training had not brought any familiar landmarks into view. These birds appear to have used type II homing at first and then shifted to something approximating type III. Pigeon No. 9 released at Batavia followed a route, described above, which suggests type II homing during the first hour, followed, after failure to reach familiar territory, by type I.

In conclusion, it must be admitted that the central problem of pigeon navigation remains unsolved; the sensory basis of orientation in both type II and type III homing is still a matter for speculation. There is, however, good reason to hope that the real progress achieved within the past few years will continue during the reasonably near future, and that the definite demonstration of these three categories of homing in pigeons may lead to their further analysis, and eventually to experiments that will clarify the sensory basis of types II and III. Indeed significant progress in this direction has been reported very recently by Kramer and his associates, who have apparently succeeded in arranging an experimental situation in which birds demonstrate

their choice of a definite compass direction while confined within a small cage. The results achieved to date point towards a sort of celestial navigation based upon the sun and sky brightness patterns; but a discussion of this subject is outside the scope of the present paper, especially since the current status of the larger subject of orientation in wild birds as well as pigeons has recently been reviewed elsewhere (Griffin, 1952).

## BIBLIOGRAPHY

- CLAPARÈDE, E.  
1903. La faculté d'orientation lointaine. Arch. de Psychol., Geneva, **2**: 133-180.
- EXNER, S.  
1905. Über das Orientierungsvermögen der Brieftauben. Sitzungsber. Kaiser. Akad. Wiss. Wien, Math.-Naturwiss. Kl. III, **114**: 763-790.
- DINNENDAHL, L., and G. KRAMER  
1950. Heimkehrleistungen italienischer und deutscher Reisetauben. Die Vogelwarte, **15**: 237-242.
- FRISCH, K. v.  
1950. Bees, their vision, chemical senses, and language. Cornell Univ. Press, Ithaca, N. Y.
- GRIFFIN, D. R.  
1940. Homing experiments with Leach's petrels. Auk, **57**: 61-74.  
1943. Homing experiments with herring gulls and common terns. Bird Banding, **14**: 7-33.  
1944. The sensory basis of bird navigation. Quart. Rev. Biol., **19**: 15-31.  
1952. Bird navigation. Biol. Rev., **27** (4): in press.
- GRIFFIN, D. R., and R. J. HOCK  
1949. Airplane observations of homing birds. Ecology, **30**: 176-198.
- GUNDLACH, R. H.  
1932. A field study of homing in pigeons. Journ. Comp. Psychol., **13**: 397-402.
- HEINROTH, O., and K. HEINROTH  
1941. Das Heimfinde-vermögen der Brieftauben. Journ. f. Ornithol., **89**: 213-256.
- HITCHCOCK, H. B.  
1950. Aerial observations of homing pigeons. Anat. Rec. **108**, (3): 571-572.  
1952. Airplane observations of homing pigeons. Proc. Amer. Philos. Soc., **96**: 270-289.
- HODGE, C. F.  
1894. The method of homing pigeons. Popular Science Monthly, **44**, (April): 758-775.
- KRAMER, G.  
1952. Experiments on bird orientation. Ibis, **94**: 265-285.
- KRAMER, G., and U. v. ST. PAUL  
1950. Ein wesentlicher Bestandteil der Orientierung der Reisetäub: Die Richtungsdressur. Zeitschr. f. Tierpsychol., **7**: 620-631.  
1952. Heimkehrleistungen von Brieftauben ohne Richtungsdressur. Zool. Anz. Suppl. Bd., **16**: 172-178.

- KRAMER, G., and H. SEILKOPF  
1950. Heimkehrleistungen von Reisetauben in Abhängigkeit vom Wetter, insbesondere vom Wind. *Die Vogelwarte*, **15**: 242-247.
- MATTHEWS, G. V. T.  
1951. The experimental investigation of navigation in homing pigeons. *Journ. Exp. Biol.*, **28**: 508-536.
- PLATT, C. S., and R. S. DARE  
1945. The homing instinct in pigeons. *Science*, **101**: 439-440.
- RABAUD, E.  
1928. How animals find their way about. (Chap. V.), Harcourt, Brace and Co., N. Y.
- RIVIÈRE, B. B.  
1929. "The homing faculty" in pigeons. *Proc. Sixth Int. Ornithol. Congr. Copenhagen, 1926*: 535-555.
- ROWAN, W.  
1946. Experiments in bird migration. *Proc. and Trans. Roy. Soc. Canada*, (3) **40**, sect. 5: 123-135.
- RÜPPELL, W.  
1944. Versuche über Heimfinden ziehender Nebelkrähen nach Verfrachtung. *Journ. f. Ornithol.*, **92**: 106-132.
- SCHÜZ, E.  
1934. Vom Storch-versuch 1933 der Vogelwarte Rossitten. *Der Vogelzug* **5**: 21-25.  
1949. Die Spät-Auffassung ostpreussischer Jungstörche in Westdeutschland durch die Vogelwarte Rossitten 1933. *Die Vogelwarte* **15**, (2): 63-78.
- SKINNER, B. F.  
1950. Are theories of learning necessary? *Psychol. Rev.*, **57**: 193-216.
- THORPE, W. H.  
1949. Recent biological evidence for the methods of bird orientation. *Proc. Linnean. Soc. London*, **160**: 85-94.
- WATSON, J. B., and K. S. LASHLEY  
1915. Homing and related activities of birds. *Papers Dept. Marine Biol. Carnegie Instit.*, **7**: 1-104. (Carn. Inst. Publ. No. 211)
- YEAGLEY, H. L.  
1947. A preliminary study of a physical basis of bird navigation. *Journ. Appl. Physics*, **18**: 1035-1063.  
1951. A preliminary study of a physical basis of bird navigation, II. *Journ. Appl. Physics*, **22**: 746-760.

Manuscript received for publication September 3, 1952.